



## The importance of willow thickets for ptarmigan and hares in shrub tundra: the more the better?

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# The importance of willow thickets for ptarmigan and hares in shrub tundra: the more the better?

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## 1 **Abstract**

2 In patchy habitats, the relationship between animal abundance and cover of a preferred habitat may change  
3 with the availability of that habitat, resulting in a functional response in habitat use. Here we investigate the  
4 relationship of two specialized herbivores, willow ptarmigan (*Lagopus lagopus*) and mountain hare (*Lepus*  
5 *timidus*), to willows (*Salix* sp) in three regions of the shrub tundra zone – northern Norway, northern  
6 European Russia and western Siberia. Shrub tundra is a naturally patchy habitat where willow thickets  
7 represent a major structural element and are important for herbivores both as food and shelter. Using faeces  
8 counts in a hierarchical spatial design and several measures of willow thicket configuration we document a  
9 functional response in the use of willow thickets by ptarmigan, but not by hare. For hares, whose range  
10 extends into forested regions, occurrence increased overall with willow cover. For willow ptarmigan,  
11 occurrence showed a strong positive relationship to willow cover and a negative relationship to thicket  
12 fragmentation in the region with lowest willow cover at landscape scale, where willow growth may be  
13 limited by reindeer browsing. In regions with higher cover, on the contrary, such relationships were not  
14 observed. Differences in predator communities among the regions may contribute to the observed pattern,  
15 enhancing the need for cover where willow thickets are scarce. Such region-specific relationships reflecting  
16 regional specificities of the ecosystem highlight the importance of large-scale investigations to understand  
17 the relationships of habitat availability and use, which is a critical issue considering that habitat availability  
18 changes quickly with climate change and human impact.

19  
20 *Key words: habitat use, habitat fragmentation, occupancy, availability, large scale*

## 21 Introduction

22 The availability of suitable habitats determines the distribution of animals at different  
23 scales (Johnson 1980; Mayor et al. 2009; Orians and Wittenberger 1991). As animals  
24 select their habitat in function of their needs for all activities required for successful  
25 reproduction and survival, the optimal habitat is in fact often composed of a mixture of  
26 patches of several habitat types (Orians and Wittenberger 1991). Different habitats may for  
27 example be optimal for foraging and for shelter or breeding, resulting in trade-off  
28 situations (e.g. Mysterud et al. 1999). Habitat and landscape selection can in such cases  
29 vary in space in relation to changes in availability of important landscape elements (Fortin  
30 et al. 2008). A positive relationship between animal abundance and cover of a particular  
31 habitat may for instance be restricted to a certain range of cover values and flatten out or  
32 even decrease at higher values, meaning that the preference for a given type of habitat may  
33 change with its availability. Such a relationship has been defined as a functional response  
34 in habitat use by Mysterud and Ims (1998). Understanding how animal abundance and  
35 habitat area are related is an important question in ecology, in particular as the availability  
36 of habitats changes quickly with climate change and human impact.

37

38 Shrubs provide important ecological functions in many open habitats, and biodiversity as  
39 well as productivity are often enhanced where shrubs are present (Ripple and Beschta  
40 2005). Willow thickets are a characteristic component of shrub tundra vegetation (Chernov  
41 and Matveyeva 1997; Walker et al. 2005) and represent a good example of a patchy  
42 habitat. Willows (*Salix* sp.) usually grow along rivers or on slopes and are often the tallest  
43 plants in the tundra landscape, which is otherwise characterized by low-statured plants  
44 (Pajunen 2009; Pajunen et al. 2010). The thickets represent a major structural element and  
45 are highly productive habitats compared to the surrounding open tundra vegetation. They

46 play an important role in ecosystem functioning, providing food, shelter and/or breeding  
47 sites for numerous species of insects, birds and mammals (den Herder et al. 2004, 2008;  
48 Ims et al. 2007; Henden et al. 2010). Under global change, the growth of shrubs is  
49 increasing in the tundra, and shrubs are expanding northwards (Sturm et al. 2001; Tape et  
50 al. 2006; Wookey et al. 2009). At the same time in some parts of the Arctic willow growth  
51 is reduced and thickets are fragmented due to intense browsing mostly by reindeer  
52 (*Rangifer tarandus*) (Den Herder et al. 2004, 2008; Forbes et al. 2009; Kitti et al. 2009).  
53 These two opposing processes lead to varying areal extent of willows in climatically  
54 comparable regions (Pajunen et al. 2010).

55  
56 Two important herbivores, the willow ptarmigan (*Lagopus lagopus*, hereafter ptarmigan)  
57 and the mountain hare (*Lepus timidus*, hereafter hare) can be considered as willow  
58 specialists in Arctic environments. Ptarmigan depend strongly on willow shrubs, which  
59 constitute their most important food resource (West and Meng 1966; Andreev 1988; Elson  
60 et al. 2007; Hakkarainen et al. 2007) and provide cover in an otherwise barren landscape,  
61 in particular in winter (Estaf'ev and Mineev 1984; Tape et al. 2010). Recently, Henden et  
62 al. (submitted) documented increased occurrence of ptarmigan in patches with higher cover  
63 of willow thickets in north-eastern Norway. At the same time, they reported a negative  
64 effect of increased fragmentation of willow thickets. Hares are a wide-spread species in the  
65 tundra and boreal forest of Eurasia (Kolosov et al. 1965; Newey et al. 2007). In the erect  
66 shrub tundra in the northern part of their range willow thickets and their direct  
67 surroundings are the optimal habitat for hare (Labutin 1988; Shtro 2006). Willow shrubs  
68 are the hares' main food plant in winter and spring (Pavlinin 1997; Newey et al. 2007),  
69 whereas they constitute a sheltered habitat for reproduction in summer (Labutin 1988).

70

71 The relationship of these two specialized herbivores to willow thickets, whose extent  
72 varies strongly between regions in the shrub tundra, represent a good model system to  
73 investigate whether habitat use changes in relation to availability. The aim of our study is  
74 to determine whether regional abundance of ptarmigan and hare and the intensity of use  
75 (i.e. selection) of willow habitats, changes with the availability of this habitat, which is  
76 liable to change in response to impacts of climate and the abundance of browsing  
77 ungulates. Building on the study of Henden et al. (submitted) on ptarmigan in Finnmark,  
78 northernmost Norway, we applied the same method – counts of fecal pellets on permanent  
79 plots in replicate riparian landscapes – in two comparable tundra regions in the Russian  
80 Arctic. The three regions form a gradient in the amount of willow thickets. Specifically we  
81 asked whether there was a general positive relationship between the amount of willows at a  
82 large scale (landscape scale) and the occurrence of ptarmigan and hare, and whether these  
83 two herbivores consistently preferred habitats at the edge of willow thickets, also in regions  
84 with more willows. In a second step we investigated whether the positive effect of willow  
85 cover and the negative effect of fragmentation at a smaller local scale on the presence of  
86 ptarmigan reported by Henden et al. (submitted) were also observed in regions with more  
87 willow thickets, and whether hare reacted in the same way to differences in the  
88 configuration of willow thickets.

89

## 90 **Material and methods**

### 91 **Study areas**

92 The study was carried out in three regions within the southern arctic shrub tundra zone  
93 (Walker et al. 2005): Finnmark in north-eastern Norway (Fig. 1; 70.4°N, 29°E), the  
94 Nenetsky Ridge in Nenetsky Autonomous Okrug, Russia (68.3°N, 53.3°E) and southern  
95 Yamal, Russia (68.2°N, 69.1°E).

96

97 The study area in Finnmark has been described in detail in Henden et al. (2010) and  
98 Killengreen et al. (2007). The climate in this area is characterized by relatively mild  
99 winters due to the influence of the North Atlantic current and permafrost occurs only very  
100 scattered (Virtanen et al. 1999). Mean January temperature is  $-12.2^{\circ}\text{C}$  and mean July  
101 temperature is  $12.3^{\circ}\text{C}$ . Mean annual precipitation is 455 mm, of which approximately 50%  
102 falls during the snow free period (meteostation Rustefjelbma, Norwegian Meteorological  
103 Institute, [www.met.no](http://www.met.no)). The landscape is mountainous with elevations up to 500 m asl. and  
104 sparse vegetation above 400 m. The mountain slopes are dominated by heaths mainly  
105 composed of dwarf shrubs, whereas the valleys are more productive and willow thickets  
106 surrounded by meadows grow on the riparian plains. The thicket communities in this  
107 region resemble the forb-rich types described by Pajunen et al. 2010, but differ from them  
108 in exact species composition. The coast near tundra on Varanger Peninsula in the eastern  
109 part of the area is classified as erect dwarf shrub tundra (Walker et al. 2005), but there is  
110 large intra-zonal variation due to topography and a variety of substrate types (Virtanen et  
111 al. 1999). The western part of the area at Ifjordfjellet lies in sub-arctic alpine tundra with  
112 similar main vegetation characteristics (Killengreen et al. 2007).

113

114 Nenetsky Ridge is situated in the buffer zone of the State Nature Reserve Nenetsky. The  
115 climate in this area is noticeably affected by the Arctic Ocean (van Erden 2000). Mean  
116 January temperature is  $-18.9^{\circ}\text{C}$  and mean July temperature  $13.3^{\circ}\text{C}$  (World Meteorological  
117 Organisation: Zelenoye), with daily temperatures ranging from  $-40$  to  $30^{\circ}\text{C}$ . Mean annual  
118 precipitation is 450 mm per year, of which 65% falls as rain during the frost free season  
119 (van Erden 2000). The Pechora floodplains and surrounding areas are dominated by glacial  
120 landforms on sediment ground with poor drainage. The region is at the western limit of  
121 continuous permafrost, with an active layer depth between 30 and 80 cm (van Erden 2000).  
122 Our study area is situated on the eastern slope of Nenetsky Ridge, which consists of a

123 tundra plateau with gentle slopes reaching up to 140 m asl. The study area includes three  
124 rivers with relatively deep (up to 70 m) and narrow (ca 300 m) valleys. Two of the valleys  
125 do not have a flood plain at their bottom, and the river flows directly between the two  
126 slopes. The river valleys are dominated by willow thickets (mainly *S. glauca* and *S.*  
127 *phylicifolia*) interspersed with lush meadow vegetation characterized by high species  
128 diversity and plants of high productivity (Skogstad 2009). The thicket communities in the  
129 valleys belong to the forb-rich types of Pajunen (2010), resembling the *Salix-Trollius-*  
130 *Geranium* type and the *Salix-Comarum palustre-Filipendula ulmaria* type. Some willow  
131 thickets grow also on the plateau, interspersed with tundra vegetation.

132

133 The study area in Yamal is situated in the southern part of the Peninsula, close to the  
134 confluence of the Payutayaha and Erkutayaha rivers. The climate in southern Yamal is  
135 more continental than in the two other study areas. Mean temperature is -25.7°C in January  
136 and 8.6°C in July (Shiatov and Mazepa 1995, World Meteorological Organisation:  
137 Yaron). Mean annual precipitation is 350 mm per year, of which 70% fall as rain in the  
138 frost free season (Shiatov and Mazepa 1995). Most of the Yamal Peninsula consists of  
139 sandy and clayey marine, alluvial and lacustrine sediments (Walker et al. 2009; Pajunen  
140 2009 and literature cited therein), and permafrost is continuous in the region (Pavlov and  
141 Moskalenko 2002). Our study area is characterized by flat tundra interspersed with hills  
142 (up to 40 m high) with sometimes steep slopes, and sandy cliffs along rivers. The tundra is  
143 subdivided by a dense network of rivers and lakes, and many low lying areas are flooded  
144 in spring. The area lies at the border between erect dwarf-shrub tundra and low-shrub  
145 tundra (Walker et al. 2005). Willow thickets are sometimes interspersed with *Alnus* and  
146 form communities which are close to the *S. glauca-Carex aquatilis* type (Pajunen et al.  
147 2010). Some of the thicket communities can also be classified as *Salix lanata-myosotis*  
148 *nemorosa* type.



149

150 **Study design**

151 Our study followed a hierarchical design with several nested levels. At the largest scale we  
152 compared the three study regions (Fig. 1). The three sub-regions in Finnmark will here be  
153 treated collectively as Henden et al. (submitted) did not find ptarmigan response to willow  
154 thicket variables to differ among them. The two regions in Russia comprised one study  
155 area each. In each study region sampling plots were arranged in units (two to five; see Fig.  
156 1a), usually valleys. Within units, study plots were selected along willow thickets growing  
157 along the river as well as in the adjacent tundra (Fig. 1b-d). The selection of units and plots  
158 within units was made to cover the existing variation in willow thicket area and  
159 fragmentation within the unit. Units were separated by at least 2km. Willow thicket plots  
160 (W) and tundra plots within each unit were, as far as possible, arranged as pairs or triplets  
161 (Fig. 1b, c). Plots in tundra vegetation were thus chosen in proximity of W plots, however  
162 at least 30 m from the edge of meadows or thickets. The nearest neighbour distance  
163 between plots in the same habitat was on average 513 m (min = 129, max = 2359 m) and  
164 the distance between plots belonging to the same pair/triplet was on average 151 m (min =  
165 36 m, max = 420 m).

166

167 The vegetation on W plots, a productive meadow dominated by herbaceous dicotyledons  
168 and grasses, placed with one side along a willow thicket (Fig. 1d; Henden et al. 2010), was  
169 chosen to be as homogenous as possible within and among the different study regions and  
170 to represent the most productive parts of the ecosystem. We chose willow thickets growing  
171 on riparian plains or valley/hill slopes and which were at least 0.5 m high. Thickets  
172 growing on rocks, mires, or which were flooded were excluded (cf Henden et al. 2010).  
173 Tundra plots, on the contrary, differed among the regions. In Finnmark, tundra plots were  
174 chosen to represent the dwarf shrub heath that dominates the tundra landscapes in northern

175 Fennoscandia (Virtanen et al. 1999; Moen 1998). These heaths are mainly composed by  
176 evergreen (*Empetrum nigrum hermaphroditum*) and deciduous dwarf shrubs (*Vaccinium*  
177 spp., *Betula nana*; Ravolainen et al. 2010). In Nenetsky, tundra plots were chosen in two of  
178 the most common vegetation types: Shrub tundra plots (S) were characterized by *B. nana*  
179 and ericoid shrubs (*Vaccinium* spp, *Rhododendron tomentosum*), interspersed with sedges  
180 (*Carex* spp) and *Rubus chamaemorus*. Hummock tundra plots (H) were dominated by  
181 cottongrass tussocks (*Eriophorum* spp) interspersed with dwarf shrubs and *R.*  
182 *chamaemorus* (Skogstad 2009). In Yamal, tundra plots were also chosen in two vegetation  
183 types which dominated in the landscape: dry tundra plots (D) were characterized by ericoid  
184 dwarf shrubs, mainly *R. tomentosum* but also *Vaccinium* spp, *B. nana* and *Eriophorum* spp,  
185 whereas on moist tundra plots (M) thick layers of *Shagnum* moss dominated together with  
186 *Carex* spp and *Eriophorum* spp tussocks, interspersed with *R. chamaemorus* and *B. nana*.  
187 Most tundra plots were situated on slopes or in the upland tundra, except the moist tundra  
188 plots in Yamal, which were placed in the lower flat tundra. Because of the configuration of  
189 the landscape, most plots were not grouped as triplets in Yamal.

190

### 191 **Feces counts and willow thicket variables**

192 Ptarmigan and hares produce conspicuous fecal pellets, which can be used as index of  
193 abundance and habitat use (hare: Krebs et al. 2001; ptarmigan: Evans et al. 2007; Ims et al.  
194 2007). In Varanger, the willow ptarmigan is sympatric with the rock ptarmigan (*Lagopus*  
195 *muta*). However, the rock ptarmigan is using mainly other habitat types, at higher altitudes  
196 than considered in this study. Fecal pellets were counted in eight permanently marked  
197 small quadrates of 0.5 x 0.5 m arranged around a 15 x 15 m study plot (Fig. 1d). Counts  
198 were performed twice per year, shortly after snow melt in spring (spring) and in the second  
199 part of august/beginning of September (fall), from 2005 to 2009 in Finnmark (a few plots  
200 were excluded from the counts in 2009 because of a change in the monitoring protocol)

201 and from 2007 to 2009 in Russia. After counting, faeces were removed from the plots. As  
202 faeces had not been removed previous to spring 2007 in Nenetsky and Yamal, the counts  
203 from spring 2007 may represent cumulative use over more than one winter. This is,  
204 however, unlikely to bias the results on relative habitat use.

205

206 The areal extent and degree of fragmentation of willow thickets were derived from aerial  
207 photographs (Finnmark) as described in Henden et al. (2010), or from Quickbird satellite  
208 images with a resolution of 0.6 m (Russian regions; DigitalGlobe™ 2001). For the Russian  
209 regions, the outlines of the thickets were digitized in ArcGIS (ESRI™). Thickets were  
210 considered distinct when they were separated by an open area of at least 2 m, as such an  
211 opening could be identified with reasonable confidence on the pictures. We quantified the  
212 areal extent of willow thicket as percent willow cover in squares of 2 x 2 km (C-land) and  
213 200 x 200 m (C-loc) using the software FRAGSTATS (McGarigal et al. 2002). Squares  
214 were centred on each study plot (except for C-land in Finnmark where the measurement  
215 was centred on each unit). Thicket fragmentation was quantified as patch density (number  
216 of patches per 4 ha – PD) and edge density (meters of edge per 4 ha – ED) measured in  
217 squares of 200 x 200 m centred on each plot. An increase in both of these measures reflects  
218 increased fragmentation or shredding (cf Meffe and Carroll 1994) of willow thickets.  
219 Choice of spatial scale is important in habitat selection studies (e.g. Mayor et al. 2009;  
220 Henden et al. 2010). However, in lack of specific data on the scaling of area use of  
221 individual hares and ptarmigan in the study regions the focal scales were chosen arbitrarily  
222 based on the spatial constraints of the study design; the local scale was the largest possible  
223 avoiding overlapping willow configuration measurements, whereas the landscape scale  
224 corresponded roughly with the size of the study units.

225

226 The vertical structure of thickets at the edge of the plots was described by willow height  
227 (W-height) and density (W-density). These were measured at four points situated at 1 m  
228 inside the edge of the willow thicket along the side of the plot. Density was determined as  
229 the number of times a willow bush (leaf or branch) touched a vertical pole placed at the  
230 measuring point (point intercepts). The mean of the four measurements was taken as the  
231 value for each plot.

232

### 233 **Statistical analysis**

234 The data were analysed at two hierarchical levels for each species. First, in order to  
235 compare the effect of C-land in the three regions, the analysis was carried out at the level  
236 of the unit. Estimates of C-land originated thus from spatially non-overlapping squares for  
237 each replicate, minimizing spatial autocorrelation (Eigenbrod et al. 2010). The number of  
238 small quadrats where faeces were present was summed over all study plots belonging to  
239 the same habitat type within each unit, season and year and used as binary response  
240 variable (number of small quadrats with presence versus number of small quadrats with  
241 absence per habitat/unit/season/year, referred to as *occurrence* in the following).

242 Generalized linear mixed effects model (GLMM) with a logit link and a binomial  
243 distribution were used for the analysis. Fixed effects were C-land (for the Russian sites an  
244 average value was used for each unit), habitat, region, season and year (as factors). We  
245 used only the years with observations in all three regions (2007-2009) for the statistical  
246 analysis. In order to be applicable in all regions, habitat was coded as W versus tundra  
247 plots, thus pooling the different tundra types (T, H, S, D, M). Unit identity was used as  
248 random effect to account for repeated measurements in the same plots. C-land was  
249 standardized by scaling it with mean = 0 and standard deviation = 0.5 to make effect  
250 estimates comparable with a the two level factor habitat (Gelman and Hill 2007). The

251 preference of ptarmigan and hare for the different tundra types in the Russian regions was  
252 analysed separately using Chi-square tests.  
253  
254 Second, we considered the effect of the configuration of willow thickets directly  
255 surrounding each W plot on habitat use by herbivores. Here we summed the number of  
256 small quadrats where faeces were present among the eight small quadrats arranged around  
257 each plot, and used it as a binary response variable in GLMM as above. C-loc quantified  
258 willow cover at this scale. We used PD as measure of thicket fragmentation. On the  
259 satellite picture from Yamal it was not always easy to trace edges precisely, and we  
260 considered thus PD a more robust indicator of willow fragmentation than ED in this case.  
261 Some of the willow configuration variables were strongly correlated, such as W-height and  
262 W-density in Yamal ( $r = 0.77$ ; Electronic Supplementary Material (ESM) Table S1). We  
263 nevertheless included them into the analysis, as Smith et al. (2009) showed that in studies  
264 of habitat fragmentation it is best to include all variables despite possible correlations.  
265 Removing some of the variables can indeed lead to biased estimates given suppressor  
266 relationships between some variables (Smith et al. 2009). In addition to these four willow  
267 configuration variables, region, year and season were included as fixed effects, and plot  
268 identity was used as random effect. For all analyses, the best model was selected among  
269 eight candidate models comprising an additive model and models with interactions of  
270 willow and habitat variables with region, year or season. All willow variables were kept in  
271 all candidate models (Smith et al. 2009). In addition, an interaction of season with year was  
272 considered.  
273  
274 Statistical analyses were carried out in R version 2.9.2 (R Core development Team 2010).  
275 GLMMs were fitted using the Laplace approximation as implemented in the lme4 package  
276 (Bates et al. 2008). Log-Likelihood ratio tests were used to compare the candidate models

277 and a model was considered superior to the next simpler model when  $P < 0.05$ . Selected  
278 models were checked for constant variance of the residuals, presence of outliers and  
279 approximate normality of the random effects. A few (1 to 8) outliers were detected in the  
280 four analyses. However, as removing them did not alter the results qualitatively and only  
281 modified estimates slightly, all data were retained in the analysis.

282

## 283 **Results**

### 284 **Regional patterns of willow thicket configuration**

285 The extent, fragmentation, as well as the vertical structure of willow thickets differed  
286 considerably between the regions (Table 1). C-land was lowest in Finnmark, much higher  
287 in Nenetsky, and intermediate in Yamal. At the local scale, considering willow cover in the  
288 vicinity of W plots, the contrasts were not as strong, and C-loc was on average lowest in  
289 Yamal. The vertical structure of the willow thickets also exhibited a contrasting pattern.  
290 Willow thickets were lower in Yamal than in the two other regions, whereas thicket  
291 density was highest in Nenetsky (Table 1). Altogether the clearest contrasts in willow  
292 thicket configuration variables were between Nenetsky and the two other regions and  
293 variation among plots was smallest in Yamal (ESM Fig. S1).

### 294 **Regional patterns of herbivore abundance**

295 There were considerable differences in occurrence of ptarmigan and hare between the  
296 regions (Fig. 2). Overall, occurrence was highest in Nenetsky. Whereas ptarmigan  
297 occurred at similar levels in eastern Finnmark and in Yamal, hare was almost absent from  
298 Finnmark (Fig. 2). Therefore this region was excluded from the statistical analysis of hare  
299 occurrence. There was a clear seasonal effect for both species, with fewer faeces found in  
300 the fall (Fig. 2). Such a difference may partly be due to the difference in the length of the  
301 seasons (about two month in summer compared to the rest of the year). As the fall

302 observation was missing in 2007 and 2009 in Yamal, only spring was analysed for this  
303 region. Some variation in occurrence was also observed between years, but given the short  
304 duration of the observations from Russia we will not make inferences about multi-annual  
305 population dynamics (see Henden et al. submitted for ptarmigan in Finnmark).

### 306 **Landscape scale habitat use**

307 For ptarmigan occurrence at the large scale, the best model included an interaction between  
308 region and the two habitat variables C-land and habitat, as well as between year and  
309 season. Willow cover at the scale of units had no significant effect on the overall  
310 occurrence of ptarmigan in the Russian regions. In Finnmark on the contrary where willow  
311 cover was on average lowest (Table 1), occurrence increased with C-land (logit estimate =  
312 6.29, standard error (SE) = 2.06; ESM Fig. S2). Considering habitat, in Yamal occurrence  
313 was nearly twice as low on tundra plots as on W plots (logit estimate for T plots with W  
314 plots as reference = -0.56, SE = 0.26, odds ratio = 0.57). In Finnmark, the preference of  
315 ptarmigan for W plots was even stronger (logit estimate for T plots = -1.83, SE = 0.30,  
316 odds ratio = 0.16), whereas in Nenetsky, where willow cover was on average highest,  
317 ptarmigan clearly preferred tundra plots (logit estimate for T plots = 0.96, SE = 0.17, odds  
318 ratio = 2.62). In addition, occurrence was significantly lower in fall than in spring, an  
319 effect which was strongest in 2008 (see ESM Table S2 for complete model output). Chi-  
320 square tests showed that in Nenetsky overall ptarmigan occurrence did not differ between  
321 the two tundra types ( $X^2 = 0.11$ ,  $df = 2$ ,  $P = 0.74$ ), whereas in Yamal ptarmigan clearly  
322 avoided M plots ( $X^2 = 17.86$ ,  $df = 2$ ,  $P < 0.001$ )

323

324 The best model for hare occurrence in the Russian regions at large scale included  
325 interactions of the two habitat variables with year and the interaction between year and  
326 season. There was a general positive effect of willow cover on occurrence per unit (logit  
327 estimate = 1.66, SE = 0.31; ESM Fig. S2). There was no consistent difference between the

328 two habitat types over the years, but more hare faeces were found on W plots in 2009 in  
329 both regions (see ESM Table S3 for complete model output). As for ptarmigan, occurrence  
330 was lower in fall than in spring. The difference between the seasons was smaller in 2007  
331 than in subsequent years (ESM Table S3). Considering tundra types, hares clearly avoided  
332 M plots in Yamal ( $X^2 = 35.64$ ,  $df = 2$ ,  $P < 0.001$ ), whereas in Nenetsky they avoided S  
333 plots ( $X^2 = 13.41$ ,  $df = 2$ ,  $P < 0.001$ ). These habitat preferences were consistent over  
334 seasons (Fig. 2).

335

### 336 **Local scale habitat use**

337 Considering only willow plots and their direct surroundings (200 x 200 m), the best model  
338 for ptarmigan occurrence included interactions of the willow configuration variables with  
339 region. For Finnmark, we observed a positive effect of C-loc and a negative effect of  
340 thicket fragmentation, as reported by Henden et al. (submitted). In addition, there was a  
341 negative effect of W-height, which was not significant in the previous analysis. The  
342 estimates of the effect of W-height were, however, not very different between the two  
343 analyses, which included a different set of years and explanatory variables. The variables  
344 used were strongly correlated, reflecting the same pattern of willow configuration, but the  
345 exact choice of variables to include can modify the estimates of the other effects (Smith et  
346 al. 2009). In Nenetsky on the contrary there was no effect of any of the willow  
347 configuration variables on the occurrence of ptarmigan and the contrasts in slope with  
348 Finnmark as reference level were significant (Fig. 3; ESM Table S4). In Yamal, the effects  
349 of willow configuration were not different from those observed in Finnmark.

350

351 For hare, the best model at the local scale included interactions of the willow configuration  
352 variables with season. As fall counts were missing in Yamal, these interactions could be  
353 estimated only for Nenetsky. In Nenetsky, PD had a negative effect on hare occurrence in



354 spring (logit estimate = -1.37, SE = 0.37), but not in fall (Fig. 4). There was also a  
355 significant contrast in the effect of W-height, which was slightly negative in spring but  
356 positive in fall (Fig. 4, ESM Table S5). Considering only spring counts from both regions  
357 produced consistent results and revealed a similar negative effect of PD, indicating that in  
358 winter hares prefer less fragmented willow thickets.

## 359 Discussion

360 For ptarmigan, our analyses revealed that the importance of willow thickets for region-  
361 specific abundance and habitat use decreased with increasing willow cover both at the  
362 scale of units and at the local scale of W plots. In each region, the effects were surprisingly  
363 consistent over years and seasons. In eastern Finnmark, where willow thickets occupy only  
364 a very small proportion of the landscape, are restricted to rather narrow riparian plains and  
365 may be additionally fragmented by intense reindeer browsing (Henden et al. 2010), there  
366 was a significant positive relationship between willow cover at the large scale and the  
367 occurrence of ptarmigan. This result was in clear contrast to the Russian regions, where  
368 willow cover was higher but did not relate to ptarmigan occurrence. At the same time the  
369 preference of ptarmigan for W plots was highest in eastern Finnmark, whereas in  
370 Nenetsky, where willow cover was highest and thickets occur also on the plateau between  
371 the valleys, ptarmigan preferred tundra plots. In Yamal willow cover was intermediate and  
372 ptarmigan preferred W plots, but not as strongly as in eastern Finnmark. At the local scale  
373 of W plots and their direct surroundings, our results show that the positive effect of willow  
374 cover and negative effect of fragmentation reported by Henden et al. (submitted) for  
375 Finnmark was also observed in Yamal. In Nenetsky on the contrary, where W plots were  
376 not the preferred habitat, ptarmigan did not select plots with relatively higher willow cover  
377 and less fragmented thickets. This may be explained by the general abundance of willows

378 in Nenetsky, but also by the fact that the range of C-loc and PD did not include equally low  
379 values in Nenetsky as in the other regions (Table 1).

380

381 Altogether we thus documented a functional response in habitat choice (Mysterud and Ims  
382 1998) for ptarmigan with respect to willow thickets – an important resource both as food  
383 and as shelter. Ptarmigan, which are characteristic medium sized herbivores of the

384 typically patchy shrub tundra, show increasing preference for willow thicket edge habitats  
385 when the amount of willow thickets on the regional level decreases. Furthermore, within  
386 regions with low amount of willows (such as in eastern Finnmark) ptarmigan prefer local  
387 areas or landscape sections with a maximum amount of less fragmented willow thickets.

388 Indeed, the contrasting results between Finnmark and the two Russian sites indicate that  
389 willow thickets are a strongly limiting resource for ptarmigan in Finnmark. Whether the  
390 willows are most important in terms of forage or protective cover is unknown. However,  
391 cover may be particularly important in presence of specialized avian predators such as gyrfalcons

392 (*Falco rusticolus*, specialized on ptarmigan; Nyström et al. 2005) and golden eagle  
393 (*Aquila chrysaetos*, specialized on both ptarmigan and hares; Johnsen et al. 2007; Nyström  
394 et al. 2006). Both of these raptors are quite common year round residents in Finnmark,

395 while they are not breeding in the two Russian regions. In the Russian regions the main

396 avian predators of ptarmigan are rough-legged buzzard (*Buteo lagopus*) and peregrine

397 falcon (*Falco peregrinus*; Osmolovskaya 1948), which are both absent in winter. In

398 addition, snowy owls (*Bubo scandiaca*) are present in all three regions in winter. The fact

399 that ptarmigan in Finnmark equally strongly selected willow thicket edges in summer and

400 in winter, although willow twigs are most foraged in winter (Tape et al. 2010), underline

401 the importance of willow thickets as cover for ptarmigan in this region. The preference for

402 willow habitats in Yamal in winter was not as strong as in Finnmark and was in fact due to

403 avoidance of the flat and *Sphagnum* dominated M plots. D plots and W plots were used

404 equally in this region, as could be expected if ptarmigan experienced lower predation  
405 pressure and thus less need for cover. The preference for tundra habitats in Nenetsky was  
406 also consistent with a reduced need for cover, and may be additionally explained by  
407 topography and landscape characteristics. Willow thickets in the deep valleys in Nenetsky  
408 are likely to be covered by thick layers of snow in winter making them less accessible for  
409 foraging than thickets on the plateau. In summer, the lush and high meadow vegetation on  
410 W plots (Skogstad 2009) may be little suitable for ptarmigan.

411  
412 In Finnmark ptarmigan preferred lower willows, but this was not the case in Nenetsky.  
413 Yamal, where willow thickets were on average lowest, was not significantly different from  
414 Finnmark in this respect, although the parameter estimate was similar to that from  
415 Nenetsky (Fig. 3), not indicating any preference for low willows. The different effect of  
416 willow height is likely to be due to different willow architecture. In Finnmark W-height  
417 and W-density were not correlated, and some of the higher shrubs had little lower branches  
418 where ptarmigan could feed. In the Russian regions willow shrubs were more dense and  
419 likely to offer equal feeding opportunities at different heights.

420  
421 As overall level of occurrence of ptarmigan was highest in Nenetsky and lower in eastern  
422 Finnmark, an alternative explanation the region-specific use of tundra habitat could be  
423 density-dependent habitat selection; i.e. that use of tundra habitats increase when the  
424 regional abundance increase due to competition for optimal habitats (e.g. Fretwell 1972).  
425 However, habitat use did not differ between the seasons although the level and mode of  
426 competition between ptarmigan is expected shift between seasons as they are territorial in  
427 summer but gather in flocks in winter (Storch 2007). Thus, we consider this explanation  
428 unlikely.

429

430 For hare, region-specific habitat selection could only be analysed in the two Russian  
431 regions where the contrast in willow cover was less. Nevertheless, our results showed that  
432 hare occurrence at the landscape scale was higher where willow cover was higher, and this  
433 effect was not different between the regions. This consistent positive effect of willow cover  
434 was in contrast to the functional response observed in ptarmigan and may be related to the  
435 distribution of hares, which extends far into the boreal and temperate zone (Kolosov et al.  
436 1965). As an animal also living in forests, hares may be less dependent on the  
437 characteristic patchy structure of shrub tundra than ptarmigan. At the same time there was  
438 no clear preference of hares for a particular habitat. Occurrence was higher on W plots in  
439 2009, but not in the two other years. At the local scale, hares preferred less fragmented  
440 thickets in winter, but this was not the case in summer. In winter, larger thickets may  
441 provide better foraging opportunities and protection. In summer on the contrary hares feed  
442 mostly in open habitats such as meadows (Labutin 1988; Pavlinin 1997), which are likely  
443 to be most accessible in a landscape with smaller willow patches.

444  
445 In addition to differences in region-specific habitat selection, our data indicated differences  
446 in regional abundance of ptarmigan and hare. The overall occurrence of ptarmigan was  
447 highest in Nenetsky and lower in Yamal and eastern Finnmark, whereas the occurrence of  
448 hares was slightly higher in Nenetsky than in Yamal, and very low in Finnmark (Fig. 2).  
449 As sampling was stratified to include main habitat types in each region, overall occurrence  
450 reflects regional abundance. When discussing ptarmigan abundance, the multi-annual  
451 population dynamics of the species should be considered (Storch 2007). In Finnmark  
452 ptarmigan numbers have consistently decreased over the last years, a decline which can  
453 neither be explained directly by willow thicket degradation or by a predator mediated  
454 effect of small rodent dynamics (Henden et al. submitted). In Yamal, the years of our study  
455 were years of low ptarmigan abundance (V. A. Sokolov, unpublished), whereas the

456 dynamics in Nenetsky are unknown. Nevertheless, overall regional abundance of both  
457 species seemed positively correlated with the amount of willow thickets, suggesting that  
458 ptarmigan and hare could be limited by the availability of thickets in Finnmark. Several  
459 non-exclusive hypotheses may explain the observed differences in regional abundance.  
460 Assuming that willow thicket growth in Finnmark is affected by intense reindeer browsing  
461 (Den Herder et al. 2004, 2008; Kitti et al. 2009), a negative impact of reindeer numbers on  
462 medium sized herbivores could be hypothesized (Ims et al. 2007). This interpretation,  
463 involving a trophic bottom-up effect, should however be completed by considerations of  
464 the predator community, which also differs between the regions. In addition to the  
465 presence of avian predators during winter (see above), red foxes (*Vulpes vulpes*) – an  
466 important predator for both hare and ptarmigan – are more abundant in Finnmark than in  
467 the Russian regions, where arctic foxes (*V. lagopus*) dominate (Killengreen et al. 2007;  
468 Arctic Predators project, unpublished). Raven (*Corvus corax*) and crow (*C. cornix*), two  
469 generalist predators which have been shown to have a negative impact on rock ptarmigans  
470 in Scotland (Watson and Moss 2004), are also considerably more abundant in Finnmark  
471 than in the Russian regions (Killengreen 2010; Arctic Predators project, unpublished).  
472 Total predation pressure is thus likely to be higher in Finnmark and may contribute to  
473 lower abundance. Our data do, however, not allow us to present more than suggestive  
474 correlations concerning regional abundance as many factors such as multi-annual  
475 population dynamics (Storch 2007; Newey et al. 2007) or the influence of hunting, which  
476 is likely to be stronger in Norway than in Russia, were not considered.

477

## 478 **Conclusions**

479 Investigating the importance of willow thickets for two medium sized herbivores in three  
480 different shrub tundra regions revealed clear differences in region specific abundance and  
481 habitat selection. We document a functional response in the use of willow habitats by

482 ptarmigan, but not for hare. Region specific relationships reflecting the regional  
483 particularities of the landscape and ecosystem highlight the importance of large scale  
484 investigations to understand the relationships of habitat availability and use, as for many  
485 other questions in ecology. Under climate change willow shrubs are likely to expand in the  
486 arctic tundra, a process which may be limited by browsing of large herbivores (Post and  
487 Pedersen 2008). Understanding how medium sized herbivores may react to changes in  
488 willow cover and thicket configuration will add an important element to predictions of how  
489 the arctic tundra ecosystem may change in the near future. Willow thickets are, however,  
490 only one component of the ecosystem influencing abundance and habitat selection of  
491 ptarmigan and hare. A complete understanding of the changes in the position of these  
492 herbivores in the tundra ecosystem will require the integration of other factors, such as  
493 predation (Lima and Dill 1990).

494

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624 Table 1. Willow thicket configuration variables presented as means and ranges (in brackets) for the three  
 625 study regions: number of plots (n), percent willow cover estimated on plots of 2x2 km (C-land), percent  
 626 willow cover estimated on plots of 200x200 m (C-loc), patch density (PD) and edge density (ED), both  
 627 measured on plots of 200x200 m.

	Finnmark	Nenetsy	Yamal
n	37	12	12
C-land (% area)	1.8 [0.6-3.5]	23.6 [17.9-30.5]	11.1 [1.2-22.7]
C-loc (% area)	19.8 [1.4-54.3]	35.0 [13.1- 52.6]	12.3 [1.5-31.9]
PD (nb patches / 4 ha)	18.5 [1-87]	29.5 [10-69]	8.5 [3.0-16.1]
ED (m edge / 4 ha)	1760 [367-4036]	2933 [1120-4908]	1021 [293-1904]
W-height (m)	1.61 [0.78-2.70]	1.70 [1.05-2.38]	0.82 [0.53-1.24]
W-density (nb of hits)	2.5 [0.3 – 5.5]	6.4 [2.3-9.5]	3.6 [2.0-6.5]

## 628 **Figure legends**

629 Fig. 1. Map of the study regions relative to the Bioclimatic subzones defined by Walker et al. (2005). In  
630 Finnmark, IF refers to Ifjordfjellet, VJ to Vestre Jakobselv and KO to Komag. The inserts show an overview  
631 of the study design: a) Three units in three small valleys in Nenetsky. b) Triplets of plots representing each of  
632 three habitat types were chosen. c) The contour of willow thickets was drawn on satellite images or aerial  
633 photographs in order to estimate their surface. d) Each plot comprised eight small quadrates where faeces  
634 were counted. Willow (W) plots were in meadows at the edge of willow thickets.

635 Fig. 2. Occurrence of faeces of willow ptarmigan and mountain hare in the three study regions is plotted for  
636 each habitat type. W – meadow plots at the edge of willow thickets, T – tundra plots in eastern Finnmark, S –  
637 shrubby tundra, H – hummock tundra, D – dry tundra and M – moist tundra (see main text for a description  
638 of the habitat types). Occurrence refers to the number of small quadrates surrounding a plot where faeces  
639 were recorded. For each year, spring and fall counts are shown.

640 Fig. 3. Local scale: ptarmigan occurrence in willow plots in the three study regions in spring 2008 as a  
641 function of willow cover and patch density in the 4 ha surrounding each plot and as a function of willow  
642 height in the plots. Points show values predicted from the selected model, and lines show relationships given  
643 average values for the other predictor variables.

644 Fig. 4. Hare occurrence in function of willow patch density in the 4 ha surrounding each plot at the edge of a  
645 willow thicket, and in function of willow height. Points show values predicted from the selected model, and  
646 lines show relationships given average values for the other predictor variables.

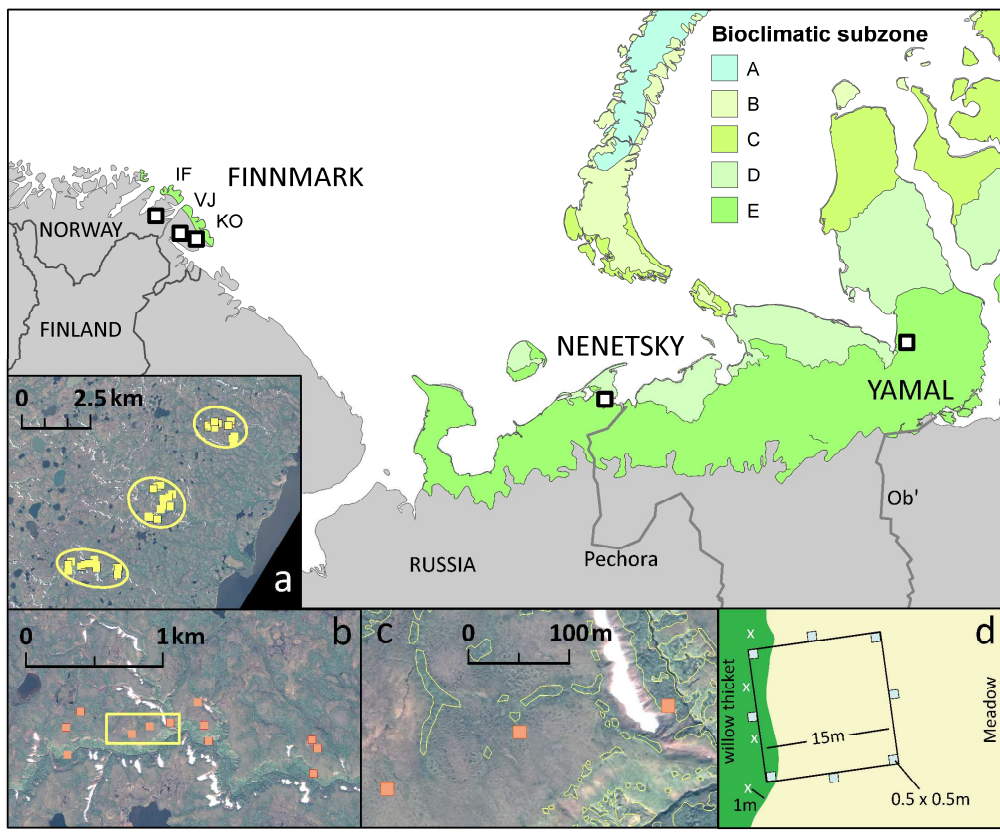


Figure 1

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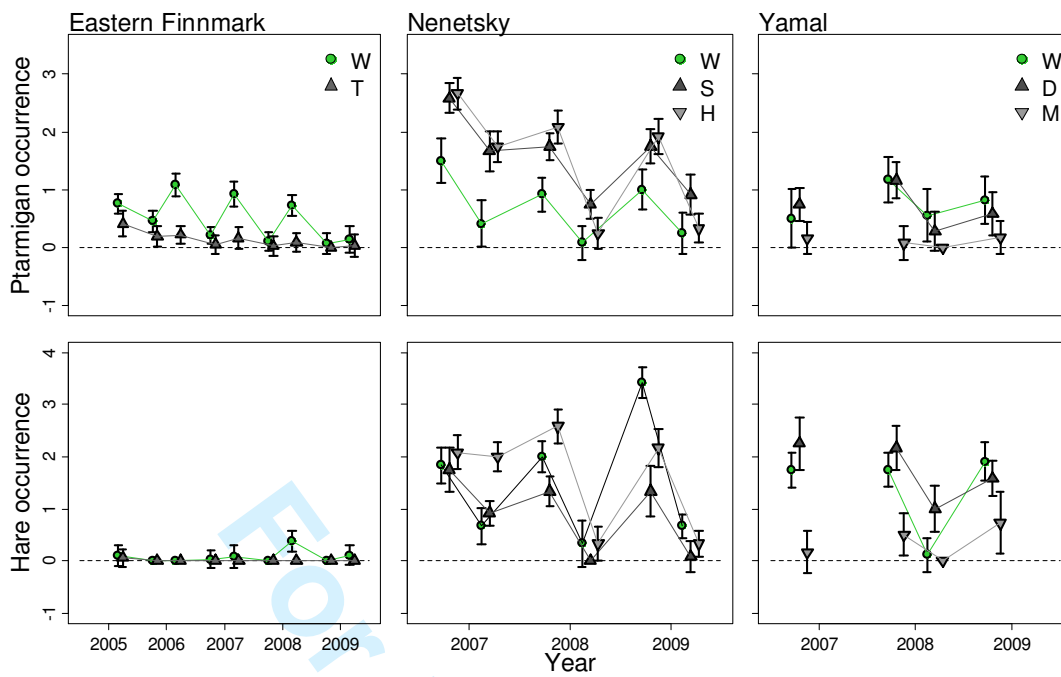


Figure 2

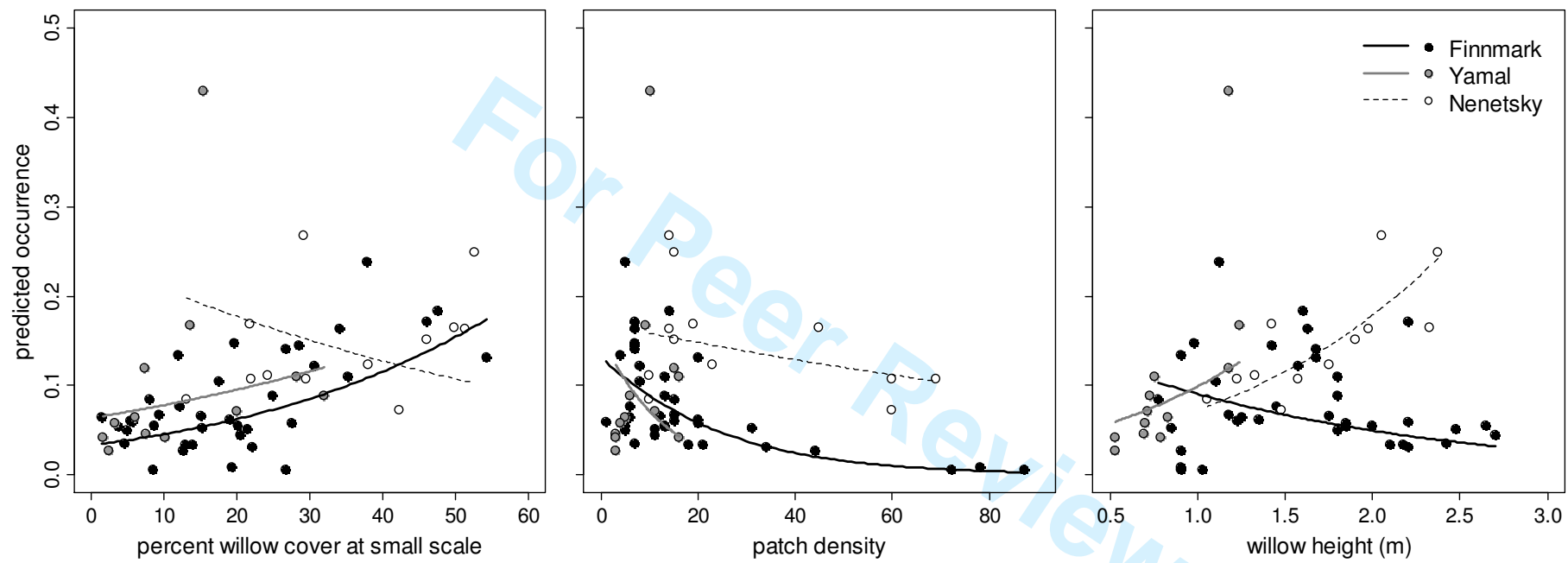


Figure 3



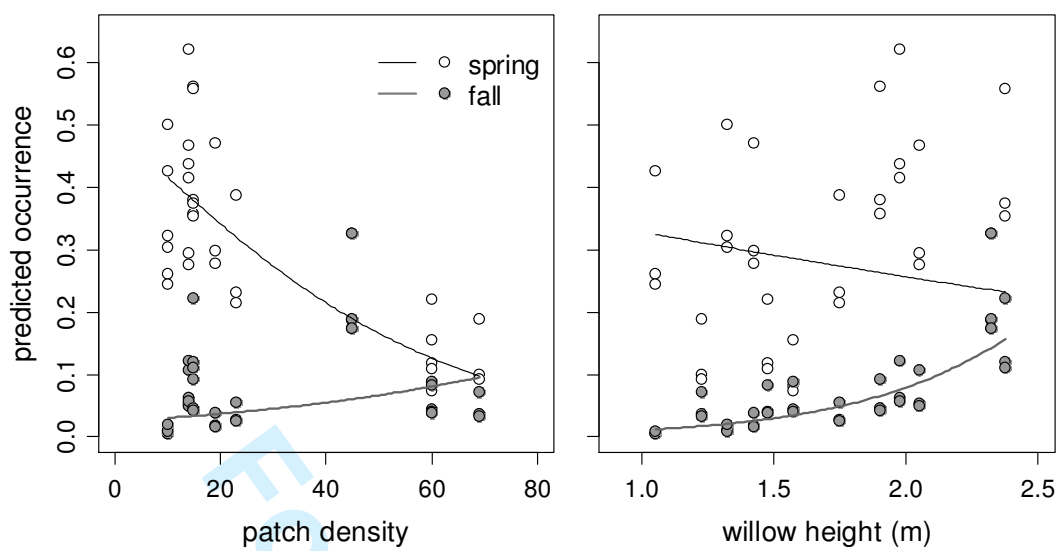


Figure 4

For Peer Review

Online supplementary Information to the paper *The importance of willow thickets for ptarmigan and hares in shrub tundra: the more the better?* By D Ehrich, JA Henden, RA Ims, L Doronina, ST Killengreen, N Lecomte, IG Pokrovsky, G Skogstad, AA Sokolov, VA Sokolov, NG Yoccoz.

**Table S1**

Correlation coefficients among the willow thicket configuration variables: C-land is the percent cover of willow thickets estimated on squares of 2x2 km, C-loc is the percent cover estimated on squares of 200x200m, PD is patch density estimated as the number of patches per 4 ha and ED is the total length of thicket edge (m) per 4 ha. Correlations are shown for the total data set as well as for each region separately. Correlation coefficients of 0.5 or more are highlighted in bold.

Total dataset

	C-loc	C-land	PD	ED	W-height
C-land	0.42				
PD	0.17	0.14			
ED	<b>0.64</b>	0.38	<b>0.77</b>		
W-height	0.36	-0.02	-0.09	0.15	
W-hits	0.37	<b>0.72</b>	0.29	0.48	0.12

Eastern Finnmark

	C-loc	C-land	PD	ED	W-height
C-land	0.52				
PD	-0.02	-0.15			
ED	0.43	0.04	<b>0.76</b>		
W-height	0.09	0.03	-0.40	-0.31	
W-hits	-0.02	0.01	0.23	<b>0.20</b>	0.02

Nenetsky

	C-loc	C-land	PD	ED	W-height
C-land	0.24				
PD	0.00	-0.19			
ED	0.46	0.18	<b>0.79</b>		
W-height	<b>0.80</b>	0.29	-0.19	0.21	
W-hits	0.38	0.16	0.18	0.42	0.40

Yamal

	C-loc	C-land	PD	ED	W-height
C-land	<b>0.57</b>				
PD	0.44	0.23			
ED	<b>0.93</b>	<b>0.50</b>	<b>0.67</b>		
W-height	0.15	0.10	0.49	0.39	
W-hits	0.37	0.40	<b>0.69</b>	<b>0.62</b>	<b>0.77</b>

**Table S2**

Results of the selected general linear mixed effects model (GLMM) for ptarmigan occurrence at the large scale in function of willow cover (C-land), habitat, region, year and season. Significant effects ( $P < 0.05$ ) are highlighted in bold. Estimates represent effects on the logit scale. Estimates of contrasts and interaction terms should be added to other contrasts for interpretation. Thus Year 2008 represents the difference between Year 2007 and Year 2008 and Habitat Tundra the difference between Habitat Willow and Habitat Tundra. The effect of C-land for occurrence in Tundra plots in Nenetsky, Spring 2007 is for example  $-2.01 + 1.02 - 0.56 - 0.54 - 0.24 + 1.52 = -0.81$ , indicating a small negative effect.

Random effect: unit, Standard deviation =  $3.38 \times 10^{-7}$   
(Number of observations: 176; number of groups: 15)

Fixed effects:

Reference levels for factors were habitat Willow, region Yamal, year 2007 and season Spring.

Effect	Estimate	Standard Error	P
<b>Intercept</b>	<b>-2.01</b>	<b>0.22</b>	<b>&lt; 0.001</b>
C-land	1.02	0.57	0.074
<b>Habitat Tundra</b>	<b>-0.56</b>	<b>0.26</b>	<b>0.034</b>
Region Nenetsky	-0.54	1.34	0.687
Region Finnmark	2.00	0.78	0.010
Year 2008	-0.22	0.14	0.123
<b>Year 2009</b>	<b>-0.59</b>	<b>0.16</b>	<b>&lt; 0.001</b>
<b>Season fall</b>	<b>-0.84</b>	<b>0.18</b>	<b>&lt; 0.001</b>
C-land x Region Nenetsky	-0.24	1.92	0.899
<b>C-land x Region Finnmark</b>	<b>5.26</b>	<b>2.14</b>	<b>0.014</b>
<b>Habitat Tundra x region Nenetsky</b>	<b>1.52</b>	<b>0.31</b>	<b>&lt; 0.001</b>
<b>Habitat Tundra x region Finnmark</b>	<b>-1.28</b>	<b>0.40</b>	<b>0.001</b>
<b>Year 2008 x season fall</b>	<b>-1.02</b>	<b>0.31</b>	<b>0.001</b>
Year 2009 x season fall	-0.46	0.31	0.138

**Table S3**

Results of the selected GLMM for hare occurrence at the large scale in function of willow cover (C-land), habitat, region, year and season. Significant effects ( $P < 0.05$ ) are highlighted in bold. Estimates represent effects on the logit scale. See legend to table 2 for interpretation of the estimates.

Random effect: unit, Standard deviation =  $5.12 \times 10^{-7}$   
(Number of observations: 72; number of groups: 5)

Fixed effects:

Reference levels for factors were habitat Willow, region Yamal, year 2007 and season Spring.

Effect	Estimate	Standard Error	P
Intercept	-0.41	0.25	0.10
<b>C-land</b>	<b>1.66</b>	<b>0.31</b>	<b>&lt; 0.001</b>
Habitat Tundra	0.09	0.19	0.617
Year 2008	0.28	0.24	0.240
<b>Year 2009</b>	<b>0.81</b>	<b>0.23</b>	<b>&lt; 0.001</b>
<b>Region Nenetsky</b>	<b>-1.30</b>	<b>0.27</b>	<b>&lt; 0.001</b>
<b>Season fall</b>	<b>-0.54</b>	<b>0.21</b>	<b>0.011</b>
C-land x Year 2008	0.08	0.29	0.778
C-land x Year 2009	0.40	0.30	0.186
Habitat Tundra x Year 2008	-0.31	0.28	0.266
<b>Habitat Tundra x Year 2009</b>	<b>0.96</b>	<b>0.27</b>	<b>&lt; 0.001</b>
<b>Year 2008 x season fall</b>	<b>1.92</b>	<b>0.44</b>	<b>&lt; 0.001</b>
<b>Year 2009 x season fall</b>	<b>-1.67</b>	<b>0.38</b>	<b>&lt; 0.001</b>

**Table S4**

Results of the selected GLMM for ptarmigan occurrence at the local scale in function of willow cover (C-loc), patch density (PD), willow height (W-height), willow density (W-density), region, year and season. Significant effects ( $P < 0.05$ ) are highlighted in bold. Estimates represent effects on the logit scale. See legend to table 2 for interpretation of the estimates.

Random effects: plot, Standard deviation = 0.149  
(Number of observations: 311; number of groups: 61)

Fixed effects:

Reference levels for factors were region Finnmark, year 2007 and season Spring.

Effect	Estimate	Standard Error	P
<b>Intercept</b>	<b>-2.29</b>	<b>0.22</b>	<b>&lt; 0.001</b>
<b>C-loc</b>	<b>0.98</b>	<b>0.25</b>	<b>&lt; 0.001</b>
<b>PD</b>	<b>-1.79</b>	<b>0.54</b>	<b>0.001</b>
<b>W-height</b>	<b>-0.71</b>	<b>0.29</b>	<b>0.015</b>
W-density	0.41	0.46	0.373
Region Nenetsky	0.54	0.42	0.191
Region Yamal	0.13	1.29	0.919
Year 2008	-0.26	0.19	0.181
<b>Year 2009</b>	<b>-0.78</b>	<b>0.23</b>	<b>0.001</b>
<b>Season Fall</b>	<b>-1.66</b>	<b>0.24</b>	<b>&lt; 0.001</b>
<b>C-loc x Region Nenetsky</b>	<b>-1.55</b>	<b>0.66</b>	<b>0.019</b>
C-loc x Region Yamal	-0.34	0.85	0.685
<b>PD x Region Nenetsky</b>	<b>1.47</b>	<b>0.64</b>	<b>0.022</b>
PD x Region Yamal	-1.66	2.58	0.519
<b>W-height x Region Nenetsky</b>	<b>1.84</b>	<b>0.82</b>	<b>0.025</b>
W-height x Region Yamal	1.99	1.54	0.120
W-density x Region Nenetsky	0.11	0.63	0.855
W-density x Region Yamal	2.92	1.20	0.057

**Table S5**

Results of the selected GLMM for hare occurrence at the local scale in Nenetsky in function of willow cover (C-loc), patch density (PD), willow height (W-height), willow density (W-density), year and season. Significant effects ( $P < 0.05$ ) are highlighted in bold. Estimates represent effects on the logit scale. See legend to table 2 for interpretation of the estimates.

Random effects: plot, Standard deviation = 0.207  
(Number of observations: 72; number of groups: 12)

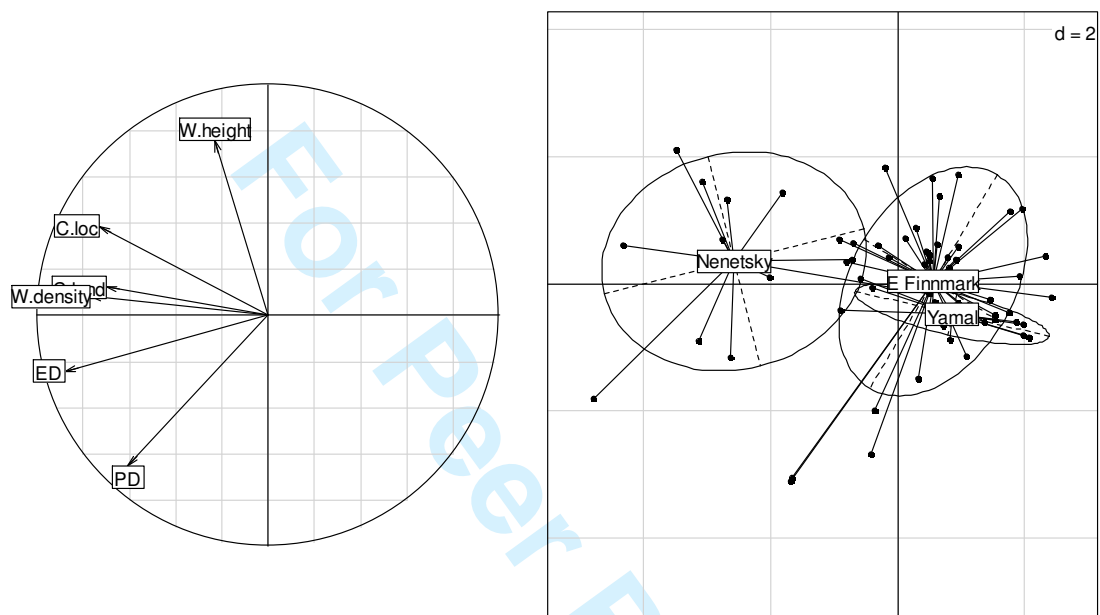
Fixed effects:

Reference levels for factors were year 2007 and season Spring.

Effect	Estimate	Standard Error	P
<b>Intercept</b>	<b>-1.18</b>	<b>0.23</b>	<b>&lt; 0.001</b>
C-loc	0.57	0.53	0.286
<b>PD</b>	<b>-1.37</b>	<b>0.37</b>	<b>&lt; 0.001</b>
W-height	-0.29	0.58	0.619
W-density	0.23	0.36	0.519
<b>Season Fall</b>	<b>-2.10</b>	<b>0.36</b>	<b>&lt; 0.001</b>
Year 2008	-0.9	0.28	0.759
<b>Year 2009</b>	<b>0.74</b>	<b>0.99</b>	<b>0.009</b>
C-loc x season Late	-0.34	0.68	0.728
<b>PD x season Late</b>	<b>2.25</b>	<b>0.99</b>	<b>0.001</b>
<b>W-height x season Late</b>	<b>1.98</b>	<b>0.76</b>	<b>0.045</b>
W-density x season Late	0.01	0.01	0.99

**Figure S1**

Principal components analysis of the willow thicket configuration variables: percent willow cover at large scale (2 x 2 km; C.land), percent willow cover at the local scale (200 x 200 m; C.loc), patch density (PD), edge density (ED), willow height (W.height) and willow density (W.density). On the left plot, arrows close to each other represent closely correlated variables. On the right plot all W plots are represented by a black dot and grouped in order to display the variation among the three regions.



**Figure S2**

Effect of willow cover at the landscape scale (units) on the occurrence of ptarmigan and hare in spring. Circles and lines indicate willow plots whereas triangles and dashed lines show tundra plots. For ptarmigan, the slope of occurrence with willow cover was different in the three regions, which are plotted in black (Finnmark), grey (Yamal) and white (Nenetsky) respectively. For hare the best model included a non significant interaction of willow cover with year. White symbols and thin lines represent 2007, light grey symbols and line 2008 and dark grey symbols and lines 2009.

